Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record

Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record

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Abstract

Accurate differentiation between tropical forest and savannah ecosystems in the fossil pollen record is hampered by the combination of: i) poor taxonomic resolution in pollen identification, and ii) the high species diversity of many lowland tropical families, i.e. with many different growth forms living in numerous environmental settings. These barriers to interpreting the fossil record hinder our understanding of the past distributions of different Neotropical ecosystems and consequently cloud our knowledge of past climatic, biodiversity and carbon storage patterns. Modern pollen studies facilitate an improved understanding of how ecosystems are represented by the pollen their plants produce and therefore aid interpretation of fossil pollen records. To understand how to differentiate ecosystems palynologically, it is essential that a consistent sampling method is used across ecosystems. However, to date, modern pollen studies from tropical South America have employed a variety of methodologies (e.g. pollen traps, moss polsters, soil samples). In this paper, we present the first modern pollen study from the Neotropics to examine the modern pollen rain from moist evergreen tropical forest (METF), semi-deciduous dry tropical forest (SDTF) and wooded savannah (*cerradão*) using a consistent sampling methodology (pollen traps). Pollen rain was sampled annually in September for the years 1999-2001 from within permanent vegetation study plots in, or near, the Noel Kempff Mercado National Park (NKMNP), Bolivia. Comparison of the modern pollen rain within these plots with detailed floristic inventories allowed estimates of the relative pollen productivity and dispersal for individual taxa to be made (% pollen / % vegetation or 'p/v'). The applicability of these data to interpreting fossil records from lake sediments was then explored by comparison with pollen assemblages obtained from five lake surface samples.

Pollen productivity is demonstrated to vary inter-annually and conforms to a consistent hierarchy for any given year: METF > SDTF > *cerradão*. This suggests an association between pollen productivity and basic structural characteristics of the ecosystem, i.e. closed canopy *vs.* open canopy *vs.* savannah. Comparison of modern pollen and vegetation revealed that some important floristic elements were completely absent from the pollen: *Qualea* and *Erisma* (METF), *Bauhinia*, *Simira* and *Guazuma* (SDTF), and *Pouteria* and *Caryocar* (*cerradão*). *Anadenanthera* was found to be abundant in both the pollen and flora of SDTF (p/v = 3.6), while Poaceae was relatively poorly represented in *cerradão* (0.2). Moraceae, *Cecropia* and *Schefflera* were found to be over-represented palynologically in all ecosystems. Overall, the data demonstrated that no one taxon could be used as a definitive indicator of any of the ecosystems. Instead, associations of taxa were found to be important: METF = Moraceae (>40%), *Cecropia*, *Hyeronima*, *Celtis*; SDTF = *Anadenanthera*, *Apuleia*, *Ferdinandusa* and non-arboreal Asteraceae, Bromeliaceae, *Piper* and fern spores; *cerradão* = Poaceae, Myrtaceae, *Borreria*, *Solanum* plus Asteraceae and fern spores. Interpretation of Poaceae pollen was highlighted as problematic, with relatively low abundance in the *cerradão* (<20%) in comparison to high abundance in lake environments (c. 30-50%). Re-examination of fossil pollen records from NKMNP revealed that modern vegetation associations were only established in the last few thousand years.

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1. Introduction

The Late Quaternary vegetation history of much of the Neotropics remains poorly understood due to an insufficient understanding of the palaeoecological significance of fossil pollen records from this region (Bush *et al.*, 2007). Attempts to reconstruct past changes in the relative distributions of moist evergreen tropical forests (METF), seasonally dry semi-deciduous tropical forests (SDTF) and savannahs have been hampered by difficulties in distinguishing between these ecosystems in palynological studies. This is because the majority of families and genera occur in more than one of these ecosystems, and their pollen can only rarely be identified to the species level (Pennington *et al.*, 2000; Mayle, 2004, 2006; Mayle *et al.*, 2004). For example, because grass pollen cannot be identified below the family level, it is often unclear in the fossil pollen record whether peaks in this pollen type reflect upland open savannas, or instead, aquatic grasses (Bush, 2002). Given that METF, SDTF and savannah ecosystems have marked differences in climatic requirements (UNESCO, 1981), species richness (Gentry, 1988; ter Steege *et al.*, 2000), and/or carbon storage values (Adams and Faure, 1998), evidence for significant past changes in their respective geographic cover would be expected to reflect marked changes in past environmental conditions, patterns of biodiversity, and carbon storage values for the Amazon and adjacent regions (Pennington *et al.*, 2000; Mayle and Beerling, 2004; Beerling and Mayle, 2006).

The characterization of modern pollen rain assemblages from different tropical ecosystems is an essential pre-requisite for the reliable interpretation of fossil pollen records. Although the number of modern pollen rain studies of Neotropical METF (Bush, 1991; Behling *et al.*, 1997; Behling and da Costa, 2000; Bush, 2000; Bush *et al.*, 2001; Bush and Rivera, 2001; Weng *et al.*, 2004; Gosling *et al.*, 2005), SDTF (Grabandt, 1980; Rodgers III and Horn, 1996; Bush and Rivera, 1998, 2001; Bush,

2000), and savannah (Salgado-Labouriau, 1973, 1978; Ferraz-Vicentini and Salgado-Labouriau, 1996; Salgado-Labouriau *et al.*, 1997; Parizzi *et al.*, 1998; Ledru, 2002; Bastos *et al.*, 2003; Martins and Batalha, 2006), has grown significantly over the last few decades, most of these studies come from outside the Amazon lowlands and very few have explored pollen-vegetation relationships. Furthermore, different investigators have typically employed differing sampling methods and approaches, thereby rendering comparison of pollen rain data between these different studies problematic.

Here, we use a consistent methodology (artificial pollen traps) to sample the pollen rain of METF, SDTF, and wooded savannah (*cerradão*) ecosystems in southwestern Amazonia and compare these data with floristic inventories of the parent vegetation to determine pollen-vegetation relationships. Once we have determined the characteristic pollen rain signature of each of these ecosystems, we then examine whether they can be reliably differentiated from each other. Comparison between these artificial pollen trap data and surface sediment pollen spectra from five lakes (two in evergreen forest and three in semi-deciduous dry forest) provide insights into the applicability of our findings to lake systems. The spatial extent to which our findings can be applied is then tested through comparison with previously published modern and fossil pollen records from the lowland Neotropics.

2. Study area

Noel Kempff Mercado National Park (NKMNP), in north-east Bolivia, provides an ideal location for investigating a range of lowland Neotropical ecosystems for three reasons. Firstly, located toward the southern margin of Amazonia, this 15,230 km^2 ecotonal area contains a mix of apparently mature METF, SDTF and savannah ecosystems (Killeen, 1998). This high beta (ecosystem) diversity makes it possible to

sample modern pollen rain across a variety of distinct ecosystems within a relatively small area. Secondly, numerous permanent vegetation study plots have already been established and surveyed within and around the park (Killeen, 1998; Panfil, 2001). By studying the pollen rain within these vegetation study plots, we are able to draw detailed pollen-vegetation comparisons. Thirdly, fossil pollen data from two lakes within NKMNP, Laguna Bella Vista and Laguna Chaplin (Mayle *et al.*, 2000; Burbridge *et al.*, 2004), are available for reanalysis based upon the modern pollen data.

Each ecosystem within our study belongs to a floristically distinct 'ecoregion' (Figure 1; Olson *et al.*, 2001): 1) Madeira-Tapajós — dominated by METF and receives 2000-4000 mm precipitation per year with temperatures ranging from 23-27^{o}C (UNESCO, 1981). Common arboreal families are Arecaceae (ex. Palmae), Cecropiaceae, Fabaceae, Melastomataceae, Moraceae, Myristicaceae and Vochysiaceae (Boom, 1986; Killeen, 1998; Panfil, 2001). 2) Chiquitano dry forest (SDTF) – characterized by mean annual precipitation between 700 and 1600 mm and a prolonged dry season (Gentry, 1995). Fabaceae and Bignoniaceae are by far the most dominant families, whilst the Anacardiaceae, Capparidaceae, Euphorbiaceae, Flacourtiaceae, Myrtaceae, Rubiaceae and Sapindaceae are also important (Gentry, 1993a, b; Killeen *et al.*, 2006). 3) The *Cerrado* – covers c. 1,900,900 km^2, as mapped by Olson *et al.* (2001), and is a complex gradation of *terra firme* South American savannahs that equates with the *cerrado* (*sensu lato*), as defined by Eiten (1972). A wide range of climatic conditions exists across the *Cerrado* ecoregion: 1000-2000 mm precipitation per year with a pronounced dry season (April – September) and mean annual temperatures ranging from 16^{o}C to 25^{o}C (Eiten, 1972; UNESCO, 1981). Despite the diversity of form and structure at the formation level (Furley, 1999), characteristic species include *Caryocar brasiliense*, *Qualea grandiflora*, *Byrsonima coccolobifolia* and *Tabebuia*

ochracea (Killeen, 1998; Killeen *et al.*, 2003; Oliveira and Marquis, 2002). In this paper we focus on the most wooded end of this spectrum; i.e. *cerradão* 'densely wooded savannah', which has a closed or slightly open canopy as defined by Eiten (1972).

3. Study locations

Modern pollen rain was collected from within permanent vegetation study plots from each of the ecosystems (ecoregions); METF from 'Los Fierros 1' (LF-1), SDTF from 'Acuario 2' (AC-2) and densely woody savannah from 'Los Fierros *cerradão*' (FC-2). Establishment of pollen traps within these plots affords a key opportunity to determine pollen-vegetation relationships by comparison between the pollen rain data and the detailed vegetation inventories (Killeen *et al.*, 2006; www.salvias.net). The modern pollen rain from LF-1 was examined in detail by Gosling *et al.* (2005), with particular attention focused on the within-plot patterns of: i) spatial and temporal variations, ii) pollen-vegetation relationships, and iii) characteristic taxa. The findings of Gosling *et al.* (2005) are summarised below (sections 3.1 and 5.2.1) and placed in a broader ecological context through comparison with new data from AC-2 and FC-2. In addition, surface sediment samples were analysed to ascertain the nature of modern pollen deposited in a lake setting. These were Lagunas Bella Vista (13°37'S, 61°33"W) and Chaplin (14°28"S, 61°04"W), located within the Madeira-Tapajós ecoregion (METF) (Mayle *et al.*, 2000; Burbridge *et al.*, 2004), and Lagunas Mandioré (18°05"S, 57°33"W), Socórros (16°08"S, 63°07"W) and La Gaiba (17°47"S, 57°43"W), located within the Chiquitano ecoregion (SDTF) (Figure 1).

3.1 Los Fierros 1 (METF)

The LF-1 study plot (14°34'50"S, 60°49'48"W, c. 250 metres above sea level [m a.s.l.]) is 500 x 20 m and contains closed-canopy tall *terra firme* METF located within NKMNP. The vegetation of this plot is apparently mature and every plant ≥10 cm diameter breast height (d.b.h.) has been recorded and the floristic composition shown to be similar to that of the sister plot, 'Los Fierros 2', 460 m away (Panfil, 2001; Killeen *et al.*, 2003; Peacock *et al.*, 2007). Selective logging of *Swietenia* (mahogany) that has occurred within the wider region is thought to have had little effect on forest composition and structure (Killeen, 1998; Panfil and Gullison, 1998).

The important tall evergreen tree species within the plot are *Erisma uncinatum*, *Qualea paraensis* (both Vochysiaceae) and *Pseudolmedia laevis* (Moraceae), while *Phenakospermum guianensis* (Strelitziaceae), an arboreal herbaceous plant, is most abundant. Other important floristic elements are the palms, *Euterpe precatoria* and *Socratea exorrhiza* (Panfil, 2001; Gosling *et al.*, 2005). These floristic characteristics support our assertion that the LF-1 plot can be seen as representative of the tall *terra firme* METF in NKMNP and part of the wider Madeira-Tapajós ecoregion.

3.2 Acuario 2 (SDTF)

The AC-2 study plot (15°14'58"S, 61°14'42"W; c. 250 m a.s.l.), is 500 x 20 m and contains closed-canopy *terra firme* SDTF, located toward the northern limit of the Chiquitano Dry Forest ecoregion (Figure 1a). All woody stems ≥10 cm d.b.h. within the plot have been tagged and identified (Killeen *et al.*, 2006).

The three most abundant species within the plot are *Caesalpinia floribunda, Tabebuia roseo-alba,* and *Anadenanthera colubrina*, which comprise a quarter of all stems ≥10 cm d.b.h. (Table 1). The vegetation in the neighbouring 'Acuario 1' plot (parallel to AC-2, 460 metres away) is similar to that of AC-2, as revealed by

Sorensen's Index of 0.64, when based on presence/absence data, and 0.61 when based on abundance data (Killeen *et al.*, 2003). A detailed quantitative floristic analysis using 110 permanent plots in Chiquitanía and adjacent regions has shown that *Caesalpinia*, *Tabebuia*, and *Anadenanthera* are important in geographically separated regions of the Chiquitano Dry Forest but become less common in both the Amazonian and Gran Chaco forests (Killeen *et al.*, 2006). These floristic findings support our assertion that pollen rain data from our study site are likely to be representative of SDTF on a regional scale across eastern Bolivia.

3.3 Los Fierros cerradão *(densely wooded savannah)*

The FC-2 plot is a 500 m transect (permanent vegetation plot) of undisturbed *cerradão* (14°35'10"S 60°50'26"W; c. 200 m a.s.l.). A line-transect survey of stems provides detailed floristic data of vegetation cover within the plot for comparison with pollen rain data (Mostacedo and Killeen, 1997; Killeen, 1998; Panfil, 2001).

The understorey of the plot is dominated by grasses, of which there are 16 species, comprising 79% of the vegetation cover. *Trachypogon plumosus* is the most dominant species, accounting for 42% of cover (Table 2). The most abundant woody taxa (≥1% cover) are *Caraipa* aff. *densifolia* (34 occurrences), *Miconia albicans* (27 occurrences), *Tibouchina* sp. (21 occurrences) and *Ormosia* sp. (14 occurrences). In addition, this plot contains many floristic elements typical of the wider *Cerrado* ecoregion, e.g. *Myrica* (14 occurrences), *Ouratea* (14 occurrences), *Roupala* (13 occurrences), *Eriotheca* (5 occurrences), *Pouteria* (5 occurrences), *Hancornia* (4 occurrences), *Caryocar* (4 occurrences), *Bowdichia* (4 occurrences) and *Emmotum* (4 occurrences), alongside eleven genera of commonly found broadleaf shrubs and semi-shrubs (Eiten, 1972, p. 211-212).

The *cerradão* vegetation of FC-2 has some similarities with its sister plot 'Los Fierros *cerrado* (*sensu stricto*)-1' (FC-1, 14°36'16"S, 60° 51'05"W), 2.3 km south-west, as shown by Sorensen's Indices of 0.26 (presence/absence) and 0.19 (abundance) (Mostacedo and Killeen, 1997). In addition, the *cerrado* (*sensu stricto*) vegetation within NKMNP contains woody species which are prevalent across the *Cerrado* ecoregion, e.g. *Qualea grandiflora* and *Tabebuia ochracea* (Killeen, 1998).

4. Methods

4.1 Field and laboratory

To sample the pollen rain from METF (LF-1), SDTF (AC-2) and *cerradão* (FC-2) ten artificial pollen traps were deployed in each plot, each year for three years, providing a total of 30 traps per plot by the end of the three year study. These were positioned along the centre of the plots at 50 m intervals. Each pollen trap consisted of a plastic funnel, 7 cm in diameter, the outflow of which was covered by a 2.7 μm filter paper (Whatman GF/D) sealed to the plastic using putty. Above the filter paper the rest of the space within the funnel was filled with viscose rayon staple which was held in place by a coarse plastic mesh fastened across the mouth of the funnel with wire. This design allowed all pollen-sized material to be retained and water to drain freely. Each trap was mounted on a stake 50 cm above the ground, sufficiently high to ensure it was not covered by leaf litter and was clearly visible to allow for relocation. See Gosling *et al.* (2003) for further details on the trap design. Samples were collected annually, each September, over a 3 year period and are referred to by the year of their collection, i.e. 1999, 2000 or 2001.

Once collected, samples were sealed in grip-lock plastic bags and transported to the laboratory where they were stored at c. 4°C until processing using standard

techniques outlined in Faegri and Iversen (1989), with modifications detailed in Gosling *et al.* (2003). Two or three *Lycopodium* tablets were added to each sample to allow the calculation of pollen accumulation rates (Stockmarr, 1972). Pollen identifications were based primarily upon the modern pollen reference collection of c. 1000 taxa held at the University of Leicester and University of Edinburgh, compiled from herbarium material collected from the Museo de Historia Natural "Noel Kempff Mercado" (Santa Cruz, Bolivia) and the Edinburgh Royal Botanic Gardens (UK). Reference was also made to two pollen atlases (Roubik and Moreno, 1991; Colinvaux *et al.*, 1999). Nomenclature follows Killeen *et al.* (1993) with modifications for pollen taxa following Burbridge *et al.* (2004). It should be noted that although Moraceae pollen is often difficult to distinguish from Urticaceae pollen, commonly depicted in the literature as Moraceae/Urticaceae-type, we are confident in assigning 2-pore grains to Moraceae because Urticaceae in NKMNP (*Urera* and *Pouzolzia*) has 3-pore pollen grains (Burn and Mayle, 2008). Even where Moraceae/Urticaceae (3 pore) grains are encountered, these are highly likely to belong to Moraceae because Urticaceae is only rarely found in the region (Killeen, 1998; www.salvias.net).

A total of 30 trap samples (10 traps x 3 years) were collected from each plot, although it was subsequently determined that five traps per year could adequately capture the spatial variation in the pollen rain (Gosling, 2004; Gosling *et al.*, 2005). The research reported here is primarily concerned with differentiating between the pollen rain of different ecosystems, rather than the pattern of spatial variability of the pollen signal within a particular ecosystem. We have therefore aggregated the ≥100-grain pollen counts of each of the 5-10 pollen traps in a given plot in a given year to provide a total annual pollen count for each plot of ≥500 grains per year to allow inter-annual variations to be examined (Figure 2a). In addition, we present a summary 'plot' bar of

the average (mean) total land pollen (TLP) for the three years to facilitate easier comparison between pollen data from ecosystem pollen traps and lake surface sediment samples (0-1 cm below the mud-water interface, ≥300 grains TLP) from five lakes (Figure 2).

4.2 Pollen-vegetation comparisons

Modern pollen-vegetation relationships were investigated in the vegetation study plots (LF-1, AC-2, FC-2). This was achieved by comparing the pollen rain data with ecological and floristic data collected previously by Mostacedo and Killeen (1997), Panfil (2001), Killeen *et al.* (2003, 2006) and http://www.salvias.net, with particular reference to percentage occurrence of stems ≥10 cm d.b.h. in the forest plots (LF-1 and AC-2). This analysis was conducted at the plot scale, i.e. using the mean TLP from each plots three years pollen trap data.

Pollen-vegetation comparisons were made by calculating the % plot TLP / % vegetation ('p/v'). In the forest plots (LF-1 and AC-2) the vegetation value was based on number of stems (≥10 cm d.b.h.) and basal stem areas of taxa were also calculated to determine pollen production in relation to tree form and biomass (where basal area is πr^2 calculated from d.b.h.). The combination of pollen, stem, and biomass data can potentially differentiate between pollen arising from a few large trees, or instead numerous small trees, of a given taxon. In the *cerradão* (FC-2) plot, vegetation data was calculated from the percentage cover estimates from the line transect survey. It should be noted, though, that these different methods of vegetation measurement, i.e. three-dimensional biomass (based on basal area) *vs.* two-dimensional % cover, potentially complicates comparison of forest *vs.* savannah vegetation data.

We stress that the p/v ratios presented here are not intended as statistically robust calculations for the purpose of reconstructing vegetation cover from fossil pollen records. This is principally because of a poor understanding of the pollen source area, which is likely to extend beyond the plots from which the ecological data is derived (20 m wide plots). Instead, these values are intended solely as a rough guide or first-order approximation of the relative pollen productivity and dispersal of different taxa within these ecosystems.

5. Results

5.1 Modern pollen assemblages

Modern pollen assemblages from artificial pollen traps from the three vegetation study plots and surface sediment samples from five lakes are presented in Figure 2. Photographs of the most abundant taxa in the pollen rain of each of these ecosystems are shown in Figures 3 to 6.

5.1.1 Artificial pollen trap data

The pollen rain from the METF plot is dominated by Moraceae (>50% in all years) with Melastomataceae/Combretaceae present in every year >3%. Other taxa present in the pollen rain of all three years (≥1%) were *Schefflera* (ex. *Didymopanax*), *Euterpe*, *Cecropia* and *Celtis*. These taxa, plus *Alchornea*, were identified by Gosling *et al.* (2005) as the major components of the pollen rain within this plot. No one taxon dominates the modern pollen rain from the SDTF plot; *Anadenanthera* is the largest component in 1999 and 2001, and Moraceae during 2000. Both these taxa are present in all three years, along with *Schefflera*, *Attalea*, Poaceae and *Pteropsidia* (trilete) undif. (≥1%). The only two pollen types consistently present at values >3% in the *cerradão*

pollen rain are Moraceae and Poaceae. Other taxa ever-present (≥1%) in the *cerradão* plot are *Schefflera*, *Cecropia*, *Alchornea*, Melastomataceae/Combretaceae and Myrtaceae. While *Euterpe*, *Borreria* and *Solanum* are abundant (>3%) in the *cerradão* plot in one or two years (Figure 2a).

Pollen Accumulation Rates (PARs) vary widely, both between plots and inter-annually (Figure 2b). The largest individual component of the pollen rain in all plots is Moraceae, except in AC-2-99 and -01. Total PARs, considered on a year-by-year basis, show a consistent trend: METF > SDTF > *cerradão*. The two forest types show a similar inter-annual pattern in PARs; both exhibit PARs for 2000 and 2001 which are more than treble those of 1999. The PARs within the *cerradão* plot are consistently low over the 3-year study (<3000 grains cm^{-2} $year^{-1}$).

5.1.2 Lake surface-sediment data

Surface pollen samples from Lagunas Bella Vista (LBV) and Chaplin (LC), which are both within the Maderia-Tapajós moist evergreen forest ecoregion, are dominated by Moraceae (53.9% and 40.0%, respectively). Other important pollen taxa at these two sites are: *Cecropia*, Poaceae and *Celtis* (>3%) and Arecaceae undif., Cyperaceae, *Alchornea*, Melastomataceae/Combretaceae and *Pteropsidia* (monolete) undif. (consistently ≥1%). Poaceae is the major component of the modern pollen rain at Lagunas Mandioré (LM), Socórros (LS) and La Gaiba (LLG) (51.6%, 34.2% and 33.1%, respectively), all of which are within the Chiquitano semi-deciduous dry forest ecoregion, but are also adjacent to extensive grass-dominated, seasonally-flooded, savannah wetlands. Pollen of *Anadenanthera*, Moraceae and Cyperaceae is also present in all these SDTF lakes (≥1%).

5.1.3 Inter-ecosystem comparison of pollen assemblages

Seven taxa occur in traps from every year and every ecosystem (*Schefflera*, Arecaceae undif., *Cecropia*, *Alchornea*, Melastomataceae/Combretaceae, Moraceae and *Celtis*). As a proportion of the pollen (Figure 2a), Moraceae is of greater abundance in the METF (60.4% total plot, 53.9% LBV, 40.0% LC) compared with SDTF (21.3% total plot, 7.3% LM, 4.5% LS, 12.4% LLG) or *cerradão* (23.0% plot). Moraceae PAR from traps in METF is more than ten times that of the other ecosystems (Figure 2b). The other six taxa ever-present in the trap data all comprise similar proportions of the pollen assemblages in all ecosystems (Figure 2a) but all produce more pollen, i.e. have higher PARs, in the METF (Figure 2b).

Poaceae reaches its highest proportion of the pollen rain in *cerradão* pollen traps (12.3% total plot) (Figure 2a) but has highest PARs in SDTF (Figure 2b) and lowest PARs in METF traps. Lake surface sediments have consistently higher proportions of Poaceae than their trap ecosystem counterparts.

Nine taxa are found predominantly in traps from one ecosystem: METF = *Hyeronima*; SDTF = Bromeliaceae undif., *Acacia*, *Anadenanthera*, *Apuleia leiocarpa* and *Ferdinandusa eliptica*; *cerradão* = *Machaerium* type, *Borreria* and *Solanum* (Figure 2). The most abundant of these is *Anadenanthera* (25.3% total plot TLP), which is also present in all the SDTF lake surface sediments; 1.9% LM, 8.9% LS, 4.7% LLG (Figure 2a).

5.2 Modern pollen and vegetation

5.2.1. METF

Within the METF plot, Gosling *et al.* (2005) found nine floristically important woody taxa (together comprising 39.7% total stems ≥10 cm d.b.h. within the plot) to be

completely absent from the pollen rain (see Table 1 in Gosling *et al.*, 2005). Particularly noteworthy are the absence of the large canopy emergents, *Qualea paraensis* and *Erisma uncinatum*.

However, five taxa within the plot pollen rain were found to be important within the plot vegetation (see Table 2 in Gosling *et al.*, 2005). Principal among these is Moraceae (16.0% stems), which is over-represented in the pollen relative to the vegetation (pollen/vegetation, i.e. p/v = 4.0). Other floristically important taxa are relatively over- or under-represented in the plot pollen rain: *Hyeronima* (p/v = 1.7), Melastomataceae/Combretaceae (0.6), *Euterpe* (0.6), *Sloanea* (0.1), *Aspidosperma* (0.1) and *Crepidospermum* (0.03). Three taxa, *Alchornea*, *Celtis* and *Trema*, were found to be important in the modern pollen rain, but absent from the vegetation of the METF plot (stems ≥10 cm d.b.h.).

5.2.2. SDTF

The SDTF plot contains eight species identified as floristically important (stems ≥10 cm d.b.h.) that are absent from the pollen rain (Table 1). The most floristically important of these 'palynologically silent' taxa, in descending order of abundance, are: *Bauhinia rufa* (3.3% stems), *Simira cordifolia* (2.9%), *Guazuma ulmifolia* (2.7%), *Aspidosperma cylindrocarpon* (2.3%) and *Cedrela fissilis* (1.8%).

Twenty-eight taxa are represented in both the vegetation and pollen rain of this SDTF (Table 3), together comprising 74.2% of total stems ≥10 cm d.b.h. and 84.4% of total basal area. Of these twenty-eight taxa, by far the most important in the pollen rain, when expressed as a percentage abundance of the plot TLP, are: *Anadenanthera* (25.3%), Moraceae (21.3%) and Arecaceae undif. (7.3%). Other significant taxa (≥1% pollen abundance) are: *Schefflera* (3.2%), Melastomataceae/Combretaceae (1.8%),

Apuleia leocarpa (1.2%) and Myrtaceae (1.0%). All of these taxa, except Melastomataceae/Combretaceae (p/v = 0.3), are over-represented in the pollen rain relative to their abundance in the vegetation: Moraceae (p/v = 36.2), *Schefflera* (16.1), *Anadenanthera* (3.6), *Apuleia leocarpa* (2.1), Arecaceae (1.3) and Myrtaceae (1.3). Three of these pollen taxa are also important in the vegetation: *Anadenanthera* (7.0% of stems ≥10 cm d.b.h.), Melastomataceae/Combretaceae (5.7%) and Arecaceae (5.7%). Six taxa are present in the modern pollen rain at significant levels (>3%) during at least one year but are not recorded in the floristic inventory of the SDTF plot because they are grasses, herbs or small trees (Figure 2a): Asteraceae (Asteroide/Cardue) undif., *Piper*, Poaceae, *Ferdinandusa eliptica*, and *Pteropsidia* (trilete) undif.. Other non-arboreal pollen types (NAP) are also present (>1%) during the 2000 field season.

5.2.3. Cerradão

The *cerradão* plot contains eleven species that comprise at least 1% of the vegetation cover (excluding grasses) that are absent from the modern pollen rain, the most important of which are: *Caraipa* aff. *densifolia* (10.4% cover), *Ouratea boliviana* (4.3%), *Roupala montana* (4.0%), *Similax* aff. *rufescens* (2.8%), *Erythroxylum suberosum* (1.8%), *Manihot caerulescens* (1.8%) and *Pouteria ephedrantha* (1.5%) (Table 2).

Eighteen taxa are identified as present in both the pollen rain and the plot vegetation (Table 4). Superficially, it appears that the palynological representation of the vegetation is excellent with 89.4% of the vegetation cover represented in the pollen rain. However, the overwhelming majority of the cover (78.8%) comprises various species of Poaceae; consequently, only 50.0% of the non-grass cover within the plot is represented in the pollen rain. The three taxa most abundant in the pollen rain are also

the three most abundant in the flora; however, the degree of over- and under-representation of these taxa in the pollen relative to the vegetation is marked: Myrtaceae (p/v = 2.2), Melastomataceae/Combretaceae (0.8) and Poaceae (0.2) (Table 4). The most palynologically abundant taxa that are absent from the vegetation inventory of the plot are Moraceae (23.0% total plot TLP), *Solanum* (6.6%) and Arecaceae undif. (3.8%), as well as *Alchornea*, *Cecropia* and *Celtis*.

6. Discussion

6.1 Pollen-vegetation relationships

6.1.1 Ecosystem trends in pollen accumulation rates

The most striking pollen-vegetation relationship from the study plots is the difference in PAR at the ecosystem level. Regardless of which year the pollen traps were collected from, traps from the METF received more pollen per unit area than those from the SDTF, which in turn accumulated more pollen than those from the *cerradão* (Figure 2b). There are two possible reasons for this: i) the traps within the different plots are differentially retaining the pollen, or ii) the quantity of pollen rain within the ecosystems is different. If the first hypothesis is correct, this would suggest that traps within drier environments are not retaining pollen as well as those in moister environments, i.e. dry fibres allow grains to be blown out of the trap and/or drier conditions cause oxidation and breakdown of those pollen grains retained. Therefore, more damaged grains would be found in traps within the drier ecosystems, i.e. *cerradão* > SDTF > METF. However, higher quantities of damaged grains are found within the METF compared to either of the other two ecosystems (Figure 2b). In addition, METF pollen taxa are found within other ecosystems' pollen rain where no parent vegetation is present (e.g. Moraceae, *Cecropia*) but not *visa versa* (e.g. Poaceae), which suggests that

METF is a more productive system with more widespread pollen dispersal. This hierarchy of PAR values (METF > SDTF > *cerradão*) suggests that in this setting the gross pollen productivity of an ecosystem can be used to provide basic information regarding the vegetation structure, i.e. closed canopy *vs.* open canopy *vs.* savannah (*cerradão*). Consistent patterns in inter-annual variation of PARs from forest ecosystems may also hint at a broader link between ecosystem pollen productivity and climate and raise concerns over the representativeness of pollen trap data gathered over a single year (Gosling *et al*., 2005).

6.1.2 Palynologically silent taxa

Each of the study plots contained taxa identified as important components of the flora that were not represented in the modern pollen rain. A total of nine such species were present within the METF flora, eight species within the SDTF, and eleven species within the *cerradão*. Gosling *et al.* (2005) demonstrated that the palynologically silent taxa in METF could be explained through reference to the predictive hierarchy based on flower structure and pollen strategy established by Bush and Rivera (2001). The strength of this relationship is further supported by our data from SDTF and *cerradão*. For example important components of the flora found to be absent from the pollen rain of SDTF and *cerradão* either have flower structures or pollination strategies associated with low pollen productivity. For example, in SDTF *Bauhinia*, *Simira* and *Guazuma*, are all hermaphroditic (Jardim *et al.*, 2003), while in *cerradão Pouteria* is entomophilous (Pennington, 2004) and *Caryocar* is zoophilous (Mori, 2004).

6.1.3 Under-representation of taxa in the pollen rain

The p/v value for each taxon is a rough guide to the degree of its over- or under-representation in the pollen rain. In the METF, taxa that are under-represented in the pollen rain relative to their floristic abundance were shown, in the main, to hold to the hierarchy established by Bush and Rivera (2001) (Gosling *et al.*, 2005). *Acacia* (8 stems) and cf. *Cupania* (one stem) are exceptions, as they have monoecious flowers (plants have separate male and female flowers), which are usually indicative of high pollen productivity, but in this case they are poorly represented in the pollen rain (0.04% and 0.06% total plot TLP, respectively), although this may be due to the stems of these two taxa being distant from the traps, especially with regard to the single stem of *Cupania* (Table 2 in Gosling *et al.,* 2005).

In the SDTF plot nineteen taxa are under-represented in the pollen rain relative to their abundance in the vegetation (Table 3), of which thirteen have hermaphroditic flowers, four are monoecious (*Sterculia*, *Diolodendron*, *Sebastiana*, *Astronium*), and two are dioecious (plants have either male or female flowers) (Flacourtiaceae, *Lippia*) (Table 3). Dioecious plants are usually regarded as high pollen producers due to the need to disperse pollen between plants. However, under-representation of *Lippia* in the pollen rain may be due to its very small flower size and insect pollination (Atkins, 2004), while entomophily may also explain the under-representation in the pollen rain of *Sterculia*, *Diolodendron*, *Sebastiana*, and *Astronium* (Table 3).

There are fourteen under-represented taxa in the pollen rain of the *cerradão* plot relative to the flora. Of these, four are hermaphroditic (Melastomataceae/Combretaceae, *Ormosia*, *Mimosa*, cf. *Eriotheca*), five are dioecious (*Davillia*, Apocynaceae, Flacourtiaceae, *Alibertia/Amaioua*, *Lafoensia*), four may be dioecious or monoecious (Poaceae, *Matayba*, *Crotalaria*, *Galactica*), and one is monoecious (Cyperaceae) (Table 4). Twelve of these taxa are probably under-represented because they are zoophilous or

entomophilous and consequently do not produce or disperse much pollen. However, Poaceae and Cyperaceae do not conform to the predicted hierarchy of Bush and Rivera (2001) as they have pollination strategies and flower structures usually associated with high pollen productivity, i.e. they are both anemophilous (wind pollinated) and monoecious/dioecious. However, since both these families can reproduce asexually, through clonal spread, their low pollen values may reflect greater investment in this vegetative mechanism relative to sexual reproduction via flowers.

In the light of the hierarchy of Bush and Rivera (2001), the low abundance of grass pollen in the *cerradão* plot seems surprising (p/v = 0.2), even if one allows for clonal spread, although these data are not anomalous when compared with a pollen rain study of *cerradão* in Brazilia, Brazil (Ledru, 2002), which revealed similarly low grass pollen percentages (< 20%). In addition, the comprehensive study across the different structural formations within the *Cerrado (sensu lato)* ecoregion by Ledru (2002) found a gradation in the representation of grasses in the modern pollen rain, with Poaceae reaching higher pollen percentages in the more open *cerrado (sensu stricto)* and *campo cerrado* formations (>50% pollen), as one might expect. The *cerradão* data presented here and by Ledru (2002) raise the possibility of an ecosystem with grass comprising >50% cover not being dominated by grasses in their fossil pollen assemblages, indicating that caution must be exercised when interpreting the significance of Poaceae (or its absence) in the fossil pollen record.

6.1.4 Over-representation of taxa in the pollen rain

Three taxa, all tall trees, were found to be over-represented in the pollen rain of all three ecosystems: Moraceae, *Cecropia* and *Schefflera*. In the METF plot Moraceae comprises 64.3% TLP and 16.0% of the total stems in the plot (≥10cm d.b.h.), with the

anemophilous genus *Pseudolmedia* the most abundant tree (89 stems) and prolific pollen producer (p/v = 4.0, Table 2 in Gosling *et al.,* 2005). In the SDTF plot Moraceae comprises only three stems (≥10 cm d.b.h.), belonging to *Ficus eximia* (cleistogamous and wasp pollinated), *Sorocea guilleminiana* and *Maclura tinctoria* subsp. *tinctoria* (both wind pollinated). However, Moraceae pollen comprises 21.3% of the SDTF plot's TLP (p/v = 36.2), demonstrating the overwhelming pollen productivity and dispersal of *Sorocea* and *Maclura* (both dioecious, anemophilous species) compared with the other taxa within this plot. With regard to the *cerradão* plot, Moraceae was entirely absent from the vegetation inventory but comprised almost a quarter (23.0%) of the plot TLP, demonstrating both the low pollen dispersal of the savannah tree taxa, as well as the effective long-distance transport of Moraceae pollen from METF several kilometres away. Furthermore, the relatively open structure of the savannah woodland would have been conducive to the deposition of wind-blown or rained-out Moraceae pollen in the traps.

Cecropia is found in all the ecosystems' pollen rain (Figure 2) and vegetation (Killeen, 1998) although it is only recorded in the flora of the METF plot studied here. In the METF plot *Cecropia* reaches 4.4% total plot TLP and 0.4% stems (p/v = 12.3), whereas in the SDTF and *cerradão* plots it reaches 1.6% and 2.8% total plot TLP, respectively. *Cecropia* is, like Moraceae, monoecious/dioecious and anemophilous, so this over-representation can be explained through its anticipated effective long-distance dispersal, probably both within and between ecosystems.

Schefflera is present in the vegetation of all three plots at low levels (METF: two stems, SDTF: one stem, and *cerradão*: three occurrences) and is well represented in the pollen rain, which generates high p/v values for all three ecosystems: METF = 19.2, SDTF = 16.1, *cerradão* = 9.1. Although this taxon has hermaphrodite flowers (Jardim *et*

al., 2003), which are not typical of anemophilous taxa (Frodin, 2004), its high over-representation in the pollen rain can probably be attributed to its 'messy' pollination syndrome (Horn and Ramirez, 1990), whereby its very open flower structure, with large numbers of exposed anthers, results in easily dispersed pollen, possibly indicating a degree of anemophily. In addition, four other palynologically important taxa (i.e. >3% TLP) were found to be over-represented within the pollen rain relative to their abundance in the plot vegetation, probably because they also have messy pollination syndromes: *Hyeronima* (METF), *Anadenanthera* (SDTF), Arecaceae undif. (SDTF), and Myrtaceae (*cerradão*).

6.2 Palynological differentiation between ecosystems

The greater pollen productivity and effective dispersal of pollen from the METF, compared with that from SDTF and *cerradão* (Figure 2b), highlights the difficulty of differentiating ecosystems where a regional patchwork of vegetation exists. The different proportions of Moraceae in SDTF *vs.* METF is borne out in both the pollen trap and lake surface pollen samples (Figure 2a). The lakes within the Madeira-Tapajós evergreen forest ecoregion contain Moraceae values of 53.9% and 40.0%, which are several fold higher than those recorded for the lakes within the Chiquitano dry forest ecoregion, which are 7.3%, 4.5% and 12.4% (Figure 2a). These data suggest that TLP values of >40% Moraceae are required to identify METF. They also show that double figure percentages of Moraceae pollen can be found in SDTF and *cerradão* due to long distance transport from METF and/or from a few individuals locally. However, it is also true that Moraceae pollen PAR drops off very rapidly once outside the METF, i.e. c. 8,900 grains cm^{-2} within the forest but only c. 300 grain cm^{-2} in the *cerradão* plot c. 1 km away (Figure 2b); although, as a percentage of the pollen rain, the values remain

relatively high (23.0% plot *cerradão*) due to the much lower overall pollen productivity of this ecosystem.

Schefflera was identified as a good indicator of the *Cerrado* ecoregion by Ledru (2002) because of its prolific pollen production and dispersal. Our pollen data support the finding of Ledru (2002) that *Schefflera* is a high pollen producer, although its presence (and over-representation) in the pollen rain of, not only the *cerradão* (one component of the *Cerrado* ecoregion), but also SDTF and METF, demonstrates that it cannot be considered an indicator-taxon of the *Cerrado*. Four other taxa are also found in the pollen rain of all three plots (≥1%), i.e. Arecaceae, *Alchornea*, Melastomataceae/Combretaceae and *Celtis* (Figure 2), although none can be considered diagnostic of any particular ecosystem.

Poaceae has been shown to be proportionally more significant in the pollen rain the more open the vegetation is, i.e. *cerradão* > SDTF > METF (Figure 2a). This pattern is true for both artificial pollen trap and lake sediment data, although Poaceae pollen is much more abundant in the lakes than the vegetation plots (Figure 2a). The high proportion of Poaceae (and Cyperaceae) pollen in the lake sediments is due to the presence of open and wetland savannah in the regional vegetation mosaic and the abundance of these two taxa around the lake shores. It should also be borne in mind that the relative contribution of aquatic taxa to the overall lake pollen assemblage is likely to depend upon the pollen productivity of the terrestrial ecosystem in the lake catchment, i.e. aquatics are more likely to mask the pollen signal from low pollen producing *cerrado* or SDTF ecosystems rather than highly productive METF. This reinforces the assertion of Bush (2002) that interpretation of Poaceae in the fossil record is often problematic and it may be appropriate, in some cases, to exclude it from the TLP sum.

The most striking ecosystem-specific taxon is *Anadenanthera* which was restricted to SDTF, occurring in all three year's plot data, with a total plot TLP value of 25.3%, and all three SDTF lakes, ranging from 1.9 to 8.9%. Once Poaceae and Cyperaceae are excluded from the lake TLP sums (as they likely reflect aquatic/wetland rather than terrestrial vegetation), *Anadenanthera* becomes more important, with recalculated values of 4.5%, 16.5% and 9.3% (Figure 2a).

Five other taxa were found to be restricted to one of the study plots (>1%): *Hyeronima* (METF), *Apuleia leocarpa*, *Ferdinandusa eliptica* (both SDTF), *Borreria* and *Solanum* (both *cerradão*). In addition, Myrtaceae was found in both SDTF and *cerradão*, but was over three times more abundant in the latter. However, the appearance of these taxa in the pollen rain of the plots was not consistent from one year to the next and they were also absent from the lake samples (Figure 2a), suggesting caution when considering these as potential ecosystem-indicator taxa. That said, *Borreria* was identified by Salgado-Labouriau (1973) as an important component of the vegetation and pollen rain elsewhere in the *Cerrado* ecoregion, so may be a good, regionally applicable, indicator of open ground; however it should be noted that *Borreria* can be found in a variety of ecological settings usually where the canopy opens out (Croat, 1978).

The separation of the arboreal (AP) and non-arboreal components (NAP) of tropical forests palynologically is not an easy task because many families or genera have species with a variety of growth forms, e.g. trees, shrubs, lianas (Gentry, 1993c). However, taxa identified as generally (Gentry, 1993c) or locally (Killeen, 1998) not being represented by trees have been categorised as non-arboreal (Figure 2) (although we recognise that some herbaceous taxa become woody or epiphytic in forested settings, which might result in an over-estimate of NAP in METF). SDTF is found to

have a higher proportion of NAP than the other two ecosystems, not withstanding grasses. Within the SDTF plot, Asteraceae, Bromeliaceae, *Piper* and fern spores are particularly important components of the NAP. Our finding of higher NAP in SDTF relative to METF is generally supported by the lake data (Figure 2a): METF lakes – 0.0% and 1.4% NAP, SDTF lakes – 1.6%, 3.0% and 4.0% NAP.

Together, all these data demonstrate that the pollen rain signals from modern METF, SDTF and *cerradão* ecosystems of NKMNP are not easily distinguished by the presence/absence of individual taxa, with *Anadenanthera* the possible exception. Therefore, an 'assemblage approach', in conjunction with a series of abundance thresholds, is best used, whereby associations of taxa that occur together in certain proportions, are indicative of a particular vegetation type; e.g. METF = > 40% Moraceae pollen, SDTF = *Anadenanthera* in association with Bromeliaceae undif. (probably *Pseudoananas sagenarius*), *Acacia*, *Apuleia leiocarpa* and/or *Ferdinandusa eliptica*, *cerradão* = Poaceae in association with taxa such as *Machaerium* type, Myrtaceae, *Borreria* and/or *Solanum.*

6.3 Comparison with previous modern pollen studies

The extent of spatial applicability of the pollen assemblages found in NKMNP is examined through comparison with modern pollen studies from comparable vegetation types elsewhere in South America. With respect to *terra firme* METF, the Moraceae/Urticaceae pollen type is remarkably consistent in its percent abundance in the pollen rain (up to c. 60%) at NKMNP (LF-1), Cuyabeno (Ecuador), and the vicinity of Manaus (Brazil) (Bush *et al.*, 2001), demonstrating the importance of this taxon in the pollen rain of METF across a broad swathe of Amazonia. However, <30% Moraceae/Urticaceae pollen at Caxiuanã (Behling and da Costa, 2000) suggests that our

METF data may be less representative of eastern Amazonia, even though four floristically important taxa of METF in NKMNP are also found in the pollen rain of this site (*Euterpe*, Melastomataceae/Combretaceae, Moraceae/Urticaceae, and *Sloanea*). Clearly, the broader scale applicability of our METF data depends upon the particular region of Amazonia in question, which is unsurprising given the floristic heterogeneity across Amazonia (ter Steege *et al.*, 2006).

Our SDTF modern pollen assemblage has marked differences from previous pollen rain studies of SDTF in: i) montane Colombia, where dominant taxa are *Pithecolobium*, *Schinus*, *Tara*, *Dodonaea*, *Clusia*, and *Escallonia* (Grabandt, 1980), and ii) Costa Rica, where there is 50% *Anacardium* type pollen and c. 5% *Quercus* and *Weinmannia* (Rodgers III and Horn, 1996). None of these taxa are present in the floristic inventory or pollen rain of our SDTF plot.

The pollen rain signal from the *cerradão* of NKMNP is similar to that found in other modern pollen study sites from the *Cerrado* ecoregion (Salgado-Labouriau, 1973; Salgado-Labouriau, 1978; Ledru, 2002) in two respects. Firstly, many key elements of the flora are poorly represented, or absent, from the pollen rain and secondly, high pollen input from nearby vegetation associations has been demonstrated to significantly 'dilute' the local pollen rain produced by the *cerrado* vegetation. Ledru (2002) identified *Byrsonima* and *Schefflera* pollen as good *cerrado* indicators. In our study both these taxa are also found in the *cerradão* pollen rain, although the *Byrsomima* pollen was found to be indistinguishable from *Machaerium* (on the basis of the local reference material collected from the study area). However, it is likely that this pollen type most likely originates from *Machaerium*, as it is more abundant than *Byrsonima* in the wooded vegetation of NKMNP; consequently, we refer to this pollen as "*Machaerium* type". The latter is well represented in the pollen rain of our *cerradão*

plot relative to its abundance in the vegetation survey (Table 4), which supports the findings of Ledru (2002), even though it is only present in low abundance (2.0% TLP, Figure 2a). In contrast to Ledru's (2002) findings, our study shows that *Schefflera* pollen has little ecological significance, because palynologically indistinguishable species of this genus are present in all three ecosystems.

6.3 Implications for fossil pollen records

Changes in the geographic distribution, and floristic and structural characteristics, of Amazonia's forests since the last glacial period have long been debated (e.g. Colinvaux *et al.*, 2000; Prado, 2000; Haffer and Prance, 2001; Cowling, 2004). The modern pollen data presented here indicate that separation of different forest and savannah ecosystems is possible, even where no major turnover in the pollen taxa is identified, i.e. through examining changes in the abundance of certain taxa (e.g. Moraceae) and/or relative changes in PAR or NAP components within an individual fossil pollen record.

The fossil pollen records from Lagunas Bella Vista (LBV) and Chaplin (LC) (Mayle *et al.*, 2000; Burbridge *et al.*, 2004) are now re-examined. During the last glacial period (LBV >13,000 cal yr BP, and LC c. 50,000 – 11,400 cal yr BP) *Machaerium* type, *Astronium*, *Paullinia/Roupala*, *Serjania* and Myrtaceae are found to be present. These taxa are found in the pollen rain of SDTF and *cerradão* today but not in the proportions found in the fossil records, suggesting that during this period the region was dominated by a dry forest and savannah mosaic unlike those seen today.

Anadenanthera appears in these fossil records during the Holocene (LBV c. 10,800 – 1550 cal yr BP, and LC 10,160 – 650 cal yr BP) and occurs with fern spores and grasses, which suggests that there are similarities with the SDTF formation seen

today. However, the absence of other dry forest taxa identified in our pollen rain study suggests that these Holocene dry forests were compositionally different from the modern Chiquitano dry forest.

Moraceae/Urticaceae pollen reaches 40% c. 1550 cal yr BP at LBV and c. 650 cal yr BP at LC, associated with rises in *Celtis*, indicating the arrival, and dominance of, METF in the catchment of these lakes, confirming the interpretation by Mayle *et al*. (2000). This rainforest expansion is the earliest pollen assemblage in these fossil records which is closely analogous with the modern pollen trap data.

In Laguna Chaplin the transition from a fossil pollen assemblage containing dry forest elements (*Anadenanthera*) to one dominated by evergreen forest elements (Moraceae) is accompanied by a relative increase in pollen influx rates (Burbridge *et al.*, 2004). The differential pollen productivity demonstrated between SDTF and METF in the pollen traps means that this can now be interpreted as supporting evidence for the late Holocene transition from a seasonally open SDTF to a permanently closed-canopy METF. The absence of any change in sedimentology, or significant change in sedimentation rates, during this transition (Burbridge *et al*., 2004) supports our interpretation that this PAR shift was driven by a change in forest floristic composition and structure rather than any change in sediment focusing, catchment in-wash, or lake area.

Re-examination of these fossil records in the light of the modern pollen data clearly demonstrates that the modern vegetation associations are relatively recent and suggests that major reorganisation of vegetation assemblages in these ecotonal areas should be anticipated for future climate changes, potentially similar in magnitude to those seen earlier in the Holocene. Despite our finding that the majority of the LBV and LC fossil pollen assemblages do not have an exact analogue match to the ecosystems

studied here, a clearer understanding of how the modern ecosystems are represented in the pollen rain has allowed us to glean further insights into these palaeoenvironmental records. This approach should be coupled with consideration of modern ecological tolerances of the taxa involved (e.g. Bush *et al.*, 2004; Punyasena *et al.*, 2007, 2008; Silman, 2007) to extract the maximum information from fossil pollen records, including assemblages without modern vegetation analogues.

7. Conclusions

There is high inter-annual variability in the pollen rain collected in the traps may indicate a close link between climate and pollen productivity and suggest that pollen trap data from a single year should be viewed with caution (Gosling *et al.* 2005). In addition, no one element of the pollen rain was found to be indicative of any particular modern day vegetation association, except for perhaps *Anadenanthera* in the SDTF and >40% Moraceae in the METF. Consequently, to achieve a robust differentiation of these ecosystems in the fossil record, analysis of an assemblage of pollen taxa and their occurrence in certain proportions must be identified to indicate the presence of an ecosystem, with particularly characteristic associations being: i) METF – Moraceae/Urticaceae (>40%), *Cecropia* (>3%), *Hyeronima*, and *Celtis*, ii) SDTF – *Anadenanthera* (>3%), *Apuleia leocarpa*, *Ferdinandusa eliptica* and non-arboreal components Asteraceae, Bromeliaceae, *Piper* and fern spores, iii) *cerradão* (densely wooded savannah) – Poaceae, Myrtaceae*, Borreria*, *Solanum* plus Asteraceae and fern spores.

Comparison between the pollen trap and lake surface sample data highlighted the importance of understanding the catchment area from which samples are taken to facilitate an accurate interpretation. Factors to be considered are likely pollen inputs

from aquatic taxa and the wider regional vegetation mosaic, with especial reference to grass pollen. In addition, the relative differences in ecosystem pollen productivity should be taken into consideration when interpreting the fossil pollen record.

Re-examination of records from Lagunas Bella Vista and Chaplin in the light of the modern pollen data show that, while dry forest elements (*Anadenanthera*) are present at these sites during the Holocene, the fossil pollen assemblages as a whole are not perfect analogue matches with the modern pollen rain of the present-day Chiquitano SDTF of eastern Bolivia. This finding is probably a reflection of both the landscape-scale mosaic of vegetation being sampled in the pollen rain collected in the lakes, and the likely reorganisation of species within forest communities over centennial-millennial timescales. The modern pollen data confirm the arrival of a closed canopy evergreen forest in NKMNP during the last few thousand years (>40% abundance of Moraceae and increased PARs).

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Captions

Table 1. List of taxa representing ≥1% of the total number of stems ≥10 cm d.b.h. in the AC-2 plot in 1997, ranked by abundance of stems. Species highlighted in **bold** are not identified in the pollen data. Basal area calculated from the d.b.h. as measured in 1997. Ceas. = Caesalpinioideae, Mim. = Mimosoideae, and Pap. = Papilionoideae. Total number of stems = 512, total basal area = 192,733 cm^2. Raw data can be downloaded from www.salvias.net.

Table 2. List of taxa representing ≥1% cover (excluding grasses) along line transect survey in the FC-2 plot (500 m transect survey, 1993), ranked by number of occurrences. Species highlighted in **bold** are not identified in the pollen data. Abbreviations as Table 1 plus ex. = excluding. Total number of occurrences recorded = 1,541, total number of occurrences recorded excluding grasses = 326. Raw data can be downloaded from www.salvias.net.

Table 3. List of taxa that are present in both the pollen rain and vegetation of the AC-2 plot in 1997 (stems ≥10 cm dbh). p/v = % plot TLP / % of total stems of all taxa in plot surveyed. Flower structure and pollinator data from (Bush, 1995; Jardim *et al.*, 2003; Atkins, 2004; Beck, 2004; Fryxell, 2004; Lohmann, 2004; Mitchell, 2004; Webster, 2004). H = Hermaphrodite, M = Monoecious, D = Dioecious, A = Anemophilous, E = Entomophilous.

Table 4. List of taxa that are present in both the pollen rain and vegetation of the FC-2 plot (500 m transect survey, 1993). p/v = % plot TLP / % cover. Flower structure and

pollinator data from (Gentry, 1993c; Bush, 1995; de Almedia *et al.*, 1998; Beck, 2004; Daly, 2004; Davis, 2004; Graham, 2004; Kubitzki, 2004; Rapini, 2004; Thomas, 2004). Abbreviations as Table 3.

Figure 1. Modern day vegetation distribution patterns in relation to the study site: a) ecoregion, b) biome. NKMNP = Noel Kempff Mercado National Park, LBV = Laguna Bella Vista, LC = Laguna Chaplin, LM = Laguna Mandioré, LS = Laguna Socórros, LLG = Laguna La Gaiba. Biomes and ecoregion definitions follow (Olson *et al.*, 2001), base data from http://geodata.grid.unep.ch.

Figure 2. Pollen and spore summary pollen diagrams: a) percentage, and b) pollen accumulation rate (PAR). Identified pollen types ≥1% in any one sample are shown. Artificial pollen trap data are shown for the following vegetation study plots: Los Fierros 1 (LF-1) METF, Acuario 2 (AC-2) SDTF, and Los Fierros *cerradão* (FC-2) (wooded savannah). The pollen rain is collected between September 1998 – September 1999 (-99), September 1999 – September 2000 (-00), and September 2000 – September 2001 (-01). Diagonally striped bars show the mean value of all three years data for each plot. Surface sediment (0-1 cm depth) pollen spectra are shown for Laguna Bella Vista (LBV), Laguna Chaplin (LC), Laguna Mandioré (LM), Laguna Socórros (LS) and Laguna La Gaiba (LLG). LBV and LC pollen data are from Mayle *et al.* (2000) and Burbridge *et al.* (2004). Pollen of the Arecaceae genera *Attalea* and *Euterpe* (grey bars) are combined to create the Arecaceae undif. curve for LF-1, AC-2 and FC-2 to allow comparison with the lake surface sediment samples where these genera have not been differentiated. *Machaerium* type pollen encompasses *Dalbergia* (Fabaceae Pap.) and *Byrsonima* (Malpighiaceae) pollen. Other NAP (non-arboreal pollen) = Herbs/shrubs

(Alismataceae *Alisma*, Anacardiaceae *Alternanthera*, Araceae undif., Asteraceae (Lactuceae) undif., Euphorbiaceae *Acalypha*, *Chamaesyce*, *Croton*, *Sebastiana*, Fabaceae (Pap.) *Crotalaria*, Lamiaceae *Hyptis*, Loranthaceae *Psittacanthus*, Onagraceae *Ludwigia*, Polygonaceae *Polygala*); weeds (Ambrosiineae *Ambrosia*, Anthemideae *Artemisia*, Lythraceae *Cuphea*, Polygonaceae *Polygonum*); lianas/vines (Dilleniaceae *Davillia*, Euphorbiaceae *Daleschampsia*, *Hevea*, Fabaceae (Pap.) *Clitoria*, *Galactia*, Hippocrataceae *Anthodon*, Malpighiaceae *Banisteriopsis*, *Dicella*, Sapindaceae *Paullinia*). * = Moraceae and Total PAR shown at 25% of all other curves. "Number of traps" indicates the number of individual pollen trap samples (each with TLP ≥100 grains) which are combined to give the aggregate pollen sum (TLP).

Figure 3. Photographs of pollen reference material from the collection at the University of Leicester and University of Edinburgh. a-d) Araliaceae *Schefflera vinosa* (ex. *Didymopanax vinosus*), e) Arecaceae *Attalea marpia*, f) Arecaceae *Euterpe precatoria*, g-h) Bromeliaceae *Aechmea castellnavii*, i-k) Cecropiaceae *Cecropia concolor*, l-o) Euphorbiaceae *Alchornea glandulosa*, p-r) Euphorbiaceae *Hyeronima alchorneoides*.

Figure 4. Photographs of pollen reference material from the collection at the University of Leicester and University of Edinburgh. a-c) Fabaceae (Caesalpinioideae) *Apuleia leiocarpa*, d-e) Fabaceae (Mimosoideae) *Acacia aroma*, f-g) Fabaceae (Mimosoideae) *Anadenanthera colubrina*, h-k) Fabaceae (Papilionoideae) *Machaerium acutifolium*, l-o) Melastomataceae *Miconia chamissois*, p-s) Combretaceae *Combretum* sp., t-w) Moraceae *Helicostylis tomentosa*, x-y) Myrtaceae *Psidium guianense*, z-A) Piperaceae *Piper aduncum*, B-E) Rubiaceae *Borreria latifolia*.

Figure 5. Photographs of pollen reference material from the collection at the University of Leicester and University of Edinburgh. a-d) Rubiaceae *Ferdinandusa elliptica*, e-h) Sapindaceae *Serjania glabrata*, i-k) Solanaceae *Solanum apaense*, l-m) Ulmaceae *Celtis pubescens*, n-o) Ulmaceae *Trema micantha.*

Figure 6. Photographs of pollen reference material from the collection at the University of Leicester and University of Edinburgh. a-d) Asteraceae *Chromolaena squalida*, e-f) Asteraceae *Lessingianthus adenophylles*, g-i) Cyperaceae *Cyperus gigantes*, j-k) Cyperaceae *Oxycaxyum cubense*, l-m) Poaceae *Mesosetum cayennense*.

Figures in attached files

1 **Table 1**

Family	Species	Number of stems	% of total stems	Total basal area (cm^2)	% of total basal area
Fabaceae – Caes.	*Caesalpinia floribunda* Tul.	60	11.72	32,773	17.02
Bignoniaceae	*Tabebuia roseo-alba* (Ridley) Sandwith	38	7.42	11,045	5.74
Fabaceae – Mim.	*Anadenanthera colubrina* (Vell.) Brenan	36	7.03	25,795	13.39
Flacourtiaceae	*Casearia gossypiosperma* Brig.	32	6.25	5,060	2.63
Combretaceae	*Combretum leprosum* Mart.	29	5.66	7,398	3.84
Arecaceae (ex. Palmae)	*Orbignya phalerata* Mart.	19	3.71	15,747	8.18
Fabaceae – Caes.	***Bauhinia rufa* (Bong.) Steud.**	**17**	**3.32**	**4,189**	**2.18**
Rubiaceae	***Simira cordifolia* (Hook. f.) Steyerm.**	**15**	**2.93**	**2,588**	**1.34**
Boraginaceae	*Cordia alliodora* (Ruíz and Pavón) Oken	14	2.73	4,793	2.49
Sterculiaceae	***Guazuma ulmifolia* Lam.**	**14**	**2.73**	**3,739**	**1.94**
Apocynaceae	***Aspidosperma cylindrocarpon* Müll. Arg.**	**12**	**2.34**	**2,746**	**1.43**
Sterculiaceae	*Sterculia apetala* (Jacq.) Karsten	11	2.15	10,229	5.31
Flacourtiaceae	*Casearia arborea* (Rich.) Urban	10	1.95	1,165	0.61
Rhamnaceae	*Rhamnidium elaeocarpum* Reisseck	10	1.95	2,738	1.42
Arecaceae (ex. Palmae)	*Scheelea princeps* (Mart.) Karsten	9	1.76	8,649	4.49
Bombacaceae	*Chorisia integrifolia* Ulbr.	9	1.76	10,340	5.37
Meliaceae	***Cedrela fissilis* Vell.**	**9**	**1.76**	**2,632**	**1.37**
Sapindaceae	*Dilodendron bipinnatum* Radlk.	9	1.76	7,020	3.65
Anacardiaceae	*Spondias mombin* L.	8	1.56	3,717	1.93
Bignoniaceae	*Arrabidea spicata* Bureau and K. Schum	7	1.37	1,091	0.57
Euphorbiaceae	*Sebastiana huallagensis* Croizat	7	1.37	1,429	0.74
Tiliaceae	***Apeiba tibourbou* Aubl.**	**7**	**1.37**	**3,042**	**1.58**
Bombacaceae	***Pseudobombax marginatum* (A. St.-Hil.) Robyns**	**6**	**1.17**	**2,569**	**1.33**
Fabaceae – Pap.	*Machaerium villosum* Vogel	6	1.17	1,123	0.58
Malpighiaceae	*Dicella macroptera* A. Juss.	6	1.17	564	0.29
Fabaceae – Pap.	*Machaerium acutifolium* Vogel	5	0.98	2,011	1.04
Tiliaceae	***Triumfetta grandiflora* Vahl**	**5**	**0.98**	**36**	**0.02**
TOTAL		410	80.08	174,226	90.47

Table 2

Family	Species	Number of occurrences	% cover	% cover (ex. grasses)
Poaceae	*Trachypogon plumosus* (Humb. & Bonpl. ex Will.) Nees	649	42.12	199.08
Poaceae	sp11	143	9.28	43.87
Poaceae	sp5	134	8.70	41.10
Poaceae	*Paspalum gemiuniflorum* Steud	78	5.06	23.93
Poaceae	*Thrasya petrosa* (Trin.) Chase	56	3.63	17.18
Poaceae	*Sporobolus cubensis* Hitchc.	52	3.37	15.95
Poaceae	*Paspalum stellatum* Humb. & Bonpl. ex Flüggé	39	2.53	11.96
Clusiaceae	***Caraipa* aff. *densifolia* Mart.**	**34**	**2.21**	**10.43**
Melastomataceae	*Miconia albicans* (Sw.) Triana	27	1.75	8.28
Poaceae	*Andropogon selloanus* (Hack.) Hack.	25	1.62	7.67
Melastomataceae	*Tibouchina* sp. 1	21	1.36	6.44
Fabaceae – Pap.	*Ormosia* sp. 1	15	0.97	4.60
Ochnaceae	***Ouratea boliviana* Tiegh.**	**14**	**0.91**	**4.29**
Poaceae	sp.3	14	0.91	4.29
Proteaceae	***Roupala montana* Aubl.**	**13**	**0.84**	**3.99**
Dilleniaceae	*Davilla grandiflora* A. St.-Hil. & Tul.	12	0.78	3.68
Flacourtiaceae	*Casearia javitensis* Kunth	10	0.65	3.07
Myrtaceae	*Myrcia subsessilis* O.Berg.	9	0.58	2.76
Poaceae	*Ichnanthus procurrens* (Nees ex Trin.) Swallen	9	0.58	2.76
Smilacaceae	***Smilax* aff. *rufescens* Griseb.**	**9**	**0.58**	**2.76**
Poaceae	*Schizachyrium sanguineum* (Retz.) Alston	7	0.45	2.15
Erythroxylaceae	***Erythroxylum suberosum* A. St.-Hil.**	**6**	**0.39**	**1.84**
Euphorbiaceae	***Manihot caerulescens* Pohl**	**6**	**0.39**	**1.84**
Fabaceae – Pap.	*Aeschynomene oroboides* Benth.	6	0.39	1.84
Bombacaceae	*Eriotheca gracilipes* (K. Schum.) Robyns	5	0.32	1.53
Myrtaceae	*Myrcia regnelliana* O. Berg.	5	0.32	1.53
Sapotaceae	***Pouteria ephedrantha* (A. C. Sm.) Radlk.**	**5**	**0.32**	**1.53**
Apocynaceae	*Hancornia speciosa* Gomes	4	0.26	1.23
Caryocaraceae	***Caryocar brasiliense* Cambess. var *intermedium***	**4**	**0.26**	**1.23**
Combretaceae	*Buchenavia* aff. *tomentosa* Eichler	4	0.26	1.23
Clusiaceae	***Kielmeyera rubiiflora* Camb.**	**4**	**0.26**	**1.23**
Fabaceae – Mim.	*Mimosa* sp. 3	4	0.26	1.23
Fabaceae – Pap.	***Bowdichia virgilioides* Kunth**	**4**	**0.26**	**1.23**
Icacinaceae	***Emmotum nitens* (Benth) Miers**	**4**	**0.26**	**1.23**
Poaceae	*Axonopus canescens* (Nees) Kuhlm.	4	0.26	1.23
TOTAL (ex. grasses)		1,435 (239)	93.12 (15.51)	440.18 (73.31)

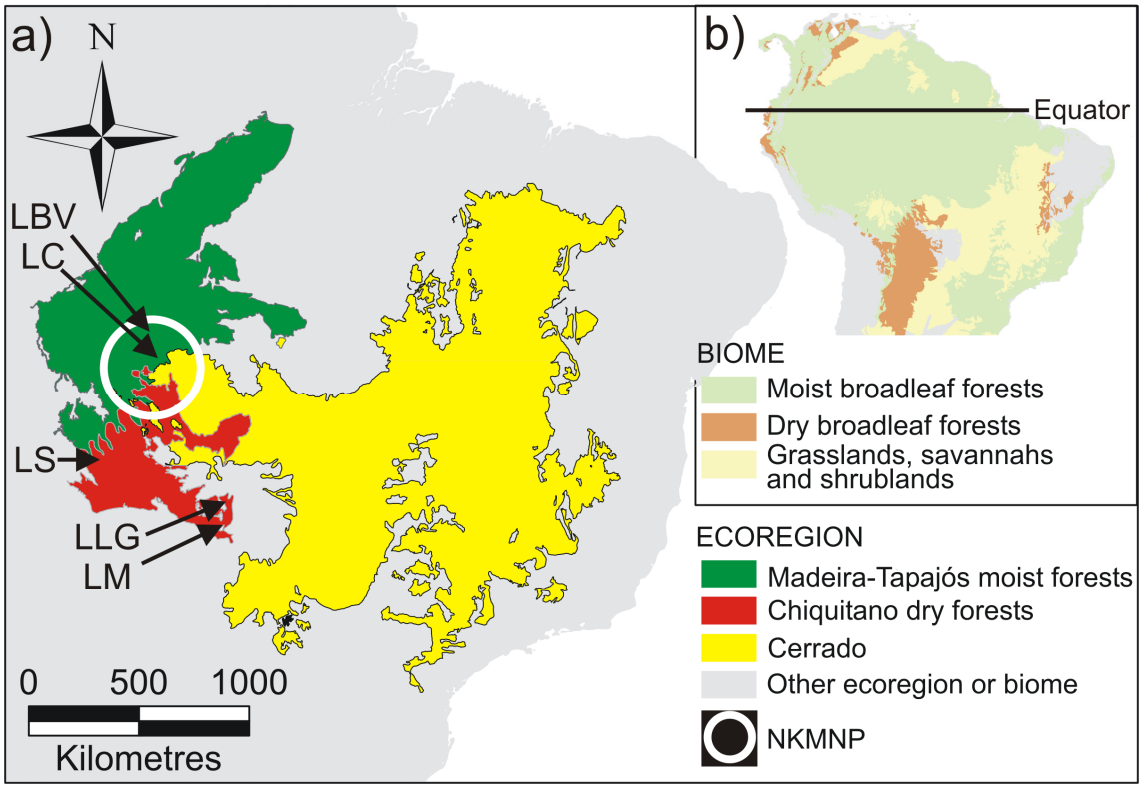
Table 3

	VEGETATION DATA				POLLEN DATA		FLOWER	
POLLEN TAXA	No. stems ≥10 cm dbh	% of total stems of all taxa in plot (v)	Total basal area (cm^2)	% total basal area	% plot TLP (p)	p/v	Structure	Pollinator
Caesalpinia undif.	60	11.72	32,773	17.01	0.21	0.02	H	E
Flacourtiaceae	46	8.98	6,593	3.42	0.11	0.01	D	E
Tabebuia cf. *roseo-alba*	38	7.42	11,045	5.73	0.02	0.00	H	E
Anadenanthera	36	7.03	25,795	13.38	25.28	3.60	H	E
Arecaceae undif.	29	5.66	24,495	12.71	7.32	1.29	M/D	E
Melastomataceae/ Combretacae	29	5.66	7,398	3.84	1.76	0.31	H	E
Bignoniaceae	19	3.71	2,556	1.33	0.06	0.02	H	E
Machaerium type	18	3.52	3,744	1.94	0.06	0.02	H	E
Cordia	17	3.32	4,842	2.51	0.40	0.12	H	E
Sterculia	11	2.15	10,229	5.31	0.13	0.06	M	E
Malpighiaceae cf. *Dicella*	10	1.95	693	0.36	0.29	0.15	H	E
Rhamnidium	10	1.95	2,738	1.42	0.15	0.08	H	E
Chorisia	9	1.76	10,340	5.37	0.06	0.03	H	E
Dilodendron	9	1.76	7,020	3.64	0.14	0.08	M	E
Spondias mombin	8	1.56	3,717	1.93	0.06	0.04	H	E
Sebastiana	7	1.37	1,429	0.74	0.12	0.09	M	E
Myrtaceae undif.	4	0.78	1,818	0.94	0.99	1.27	H	E
Tiliaceae cf. *Luehea*	4	0.78	1,286	0.67	0.03	0.04	H	E
Apuleia leocarpa	3	0.59	1,364	0.71	1.23	2.08	H	E
Moraceae	3	0.59	422	0.22	21.33	36.15	M/D	A
Serjania	3	0.59	594	0.31	0.72	1.22	H/D	E
Astronium cf. *urundava*	1	0.20	515	0.27	0.13	0.65	M	E
Schefflera	1	0.20	143	0.07	3.22	16.10	H	E
Hymenaea	1	0.20	263	0.14	0.17	0.85	H	E
Fabaceae (Mim.) cf. *Samanea tubulosa*	1	0.20	161	0.08	0.48	2.40	H	E
Amburana	1	0.20	707	0.37	0.12	0.60	H	E
Zanthoxylum	1	0.20	16	0.01	0.31	1.55	M	E
Lippia	1	0.20	10	0.00	0.05	0.25	D	E
TOTAL	380	74.22	162,705	84.42	-	-	-	-

Table 4

POLLEN TAXA	VEGETATION DATA		POLLEN DATA		FLOWER	
	No. of occurr-ences	% cover (v)	% plot TLP (p)	p/v	Structure	Pollinator
Poaceae	1,215	78.84	12.29	0.16	M/D	A
Melastomataceae/Combretaceae	55	3.57	2.85	0.80	H	E
Myrtaceae undif.	22	1.43	3.15	2.20	H	E
Ormosia	15	0.97	0.03	0.03	H	E
Davillia	12	0.78	0.12	0.15	D	E
Apocynaceae undif.	11	0.71	0.03	0.04	D	E
Flacourtiaceae undif.	11	0.71	0.06	0.08	D	E
Mimosa	7	0.45	0.12	0.27	H	E
Asteraceae (Asteroide/Cardue) undif.	5	0.32	1.47	4.59	M/D	E
Bombacaceae cf. *Eriotheca*	5	0.32	0.06	0.19	H	E
Matayba	5	0.32	0.09	0.28	M/D	E
Cyperaceae	4	0.26	0.08	0.31	M	A
Schefflera	3	0.19	1.72	9.05	H	E
Machaerium type	3	0.19	1.98	10.42	H	E
Alibertia/Amaioua	2	0.13	0.03	0.23	D	E
Crotalaria	1	0.06	0.03	0.50	M/D	E
Galactia	1	0.06	0.06	1.00	M/D	E
Lafoensia	1	0.06	0.03	0.50	D	E
TOTAL	1,378	89.42	-	-	-	-

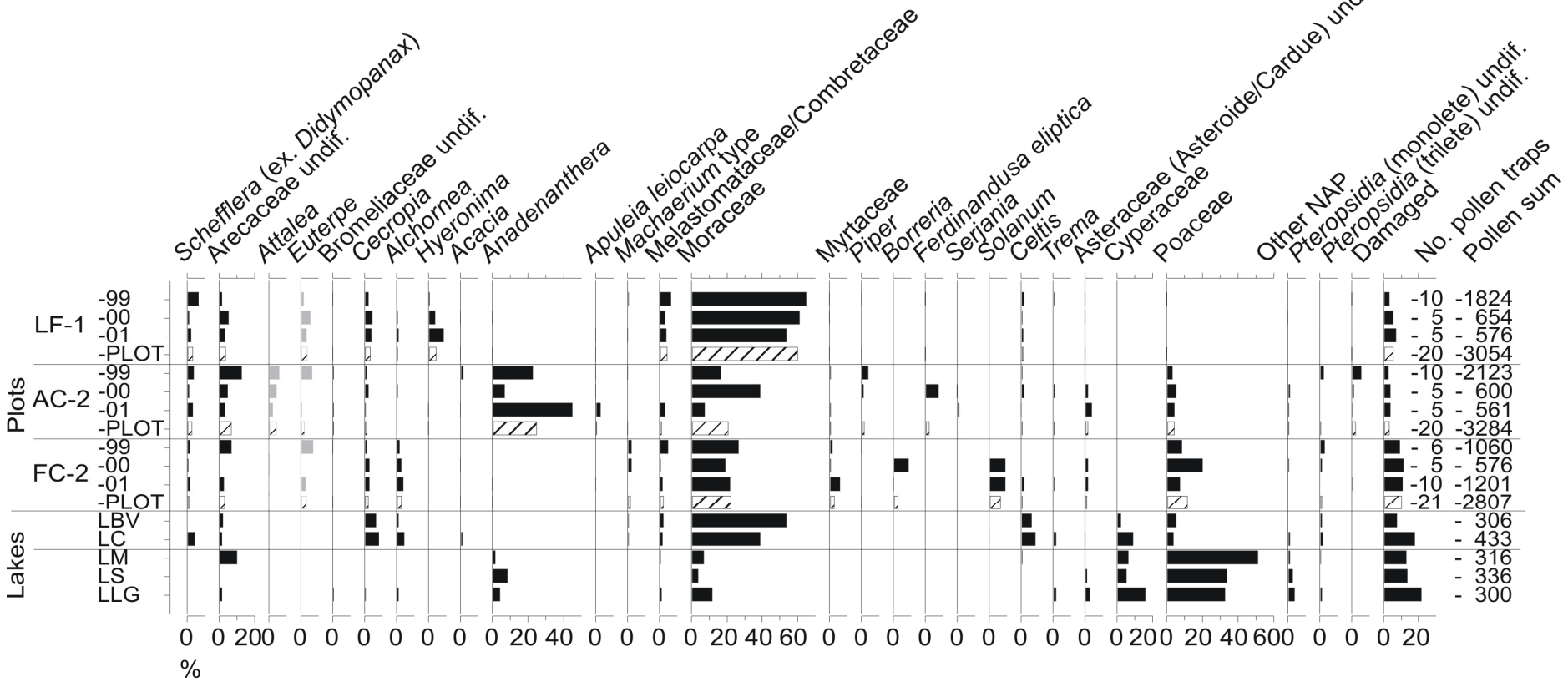
1 Figure 1


a)
N
LBV
LC
LS
LLG
LM
0
500
1000
Kilometres
b)
Equator
BIOME
Moist broadleaf forests
Dry broadleaf forests
Grasslands, savannahs and shrublands
ECOREGION
Madeira-Tapajós moist forests
Chiquitano dry forests
Cerrado
Other ecoregion or biome
NKMNP

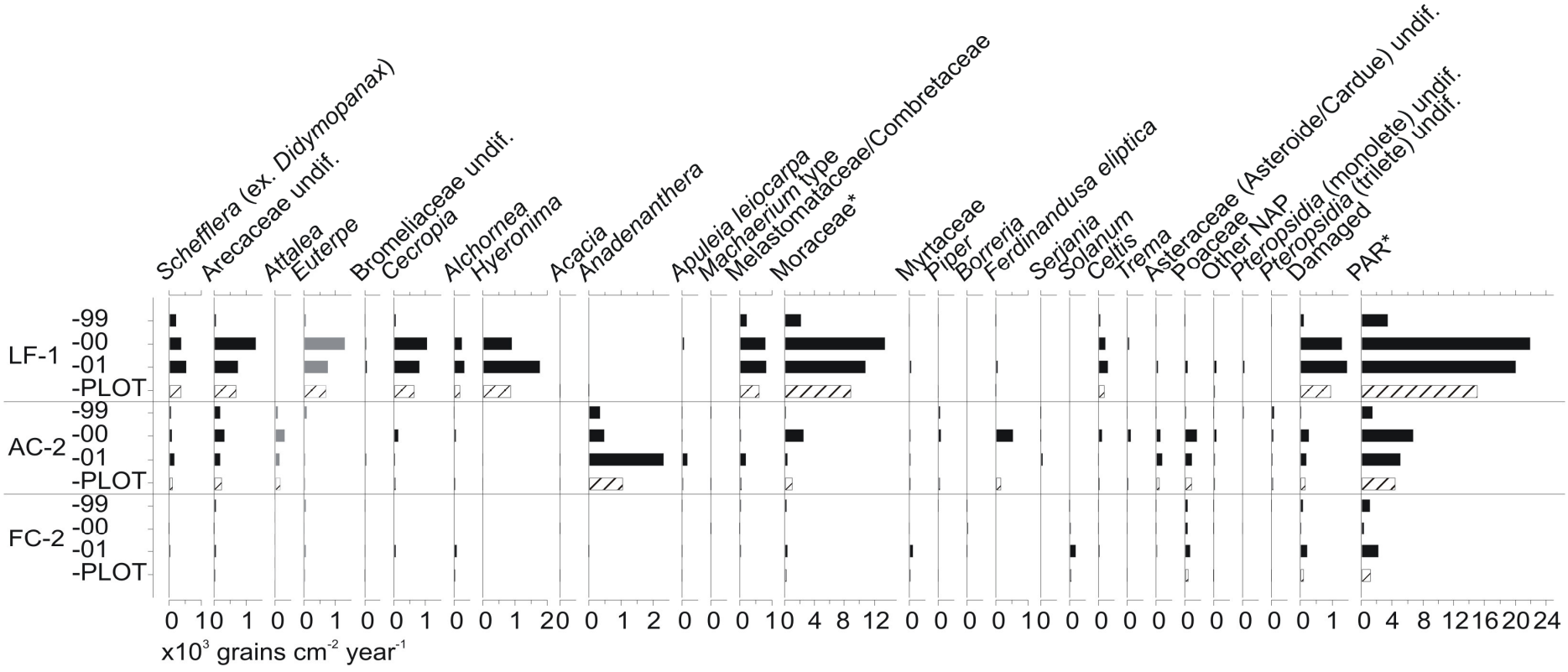
2

3

Figure 2a


Schefflera (ex. Didymopanax)
Arecaceae undif.
Attalea
Euterpe
Bromeliaceae undif.
Cecropia
Alchornea
Hyeronima
Acacia
Anadenanthera
Apuleia leiocarpa
Machaerium type
Melastomataceae/Combretaceae
Moraceae
Myrtaceae
Piper
Borreria
Ferdinandusa eliptica
Serjania
Solanum
Celtis
Trema
Asteraceae (Asteroide/Cardue) undif.
Cyperaceae
Poaceae
Other NAP
Pteropsidia (monolete) undif.
Pteropsidia (trilete) undif.
Damaged
No. pollen traps
Pollen sum
Plots
LF-1
AC-2
FC-2
Lakes
-99
-00
-01
-PLOT
LBV
LC
LM
LS
LLG
-10 -1824
- 5 - 654
- 5 - 576
-20 -3054
-10 -2123
- 5 - 600
- 5 - 561
-20 -3284
- 6 -1060
- 5 - 576
-10 -1201
-21 -2807
- 306
- 433
- 316
- 336
- 300
0 0 200 0 0 0 0 0 0 0 20 40 0 0 0 0 20 40 60 0 0 0 0 0 0 0 0 0 0 200 20 40 600 0 0 0 20
%

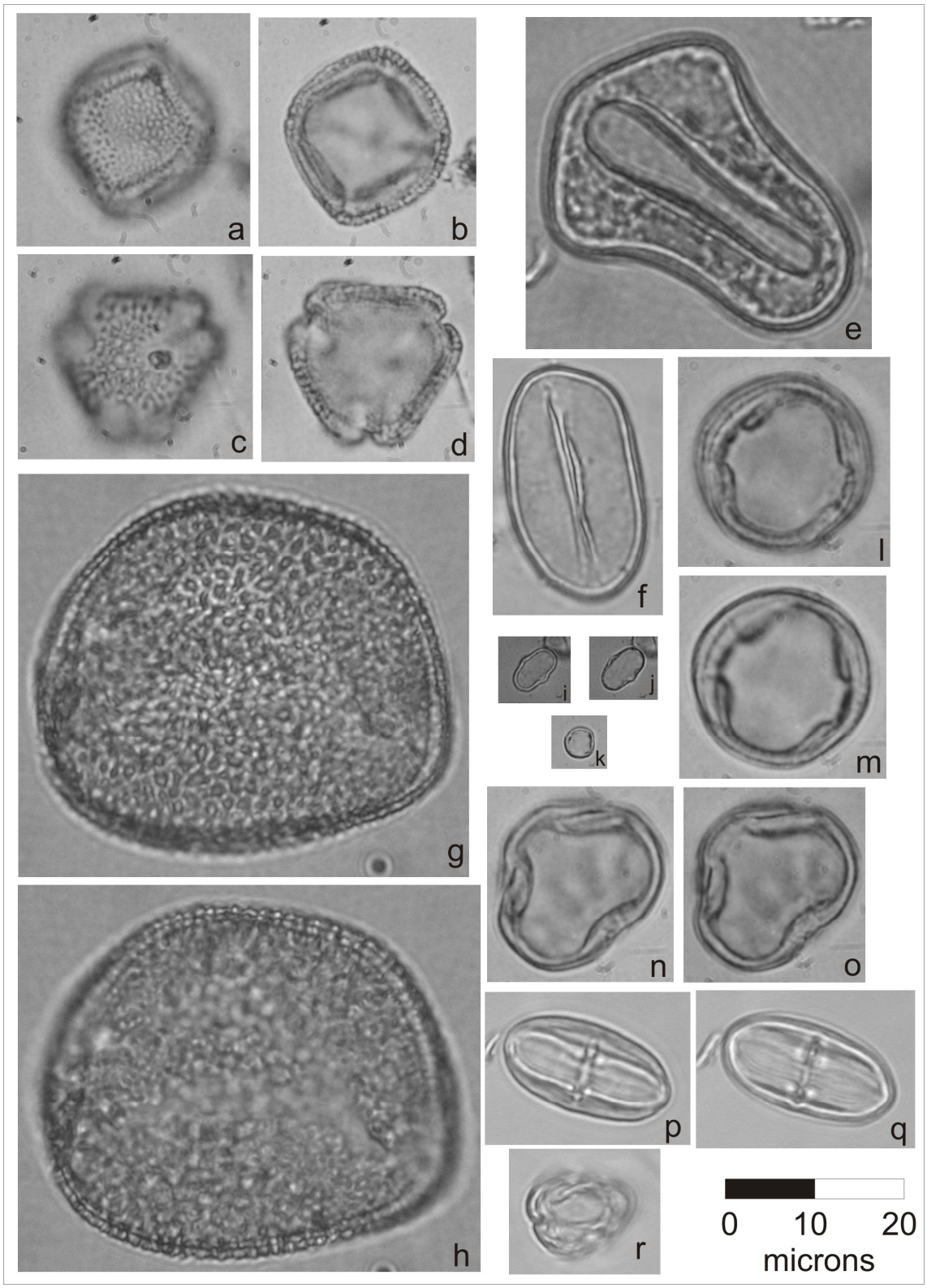
1 Figure 2b



2

3

1 Figure 3



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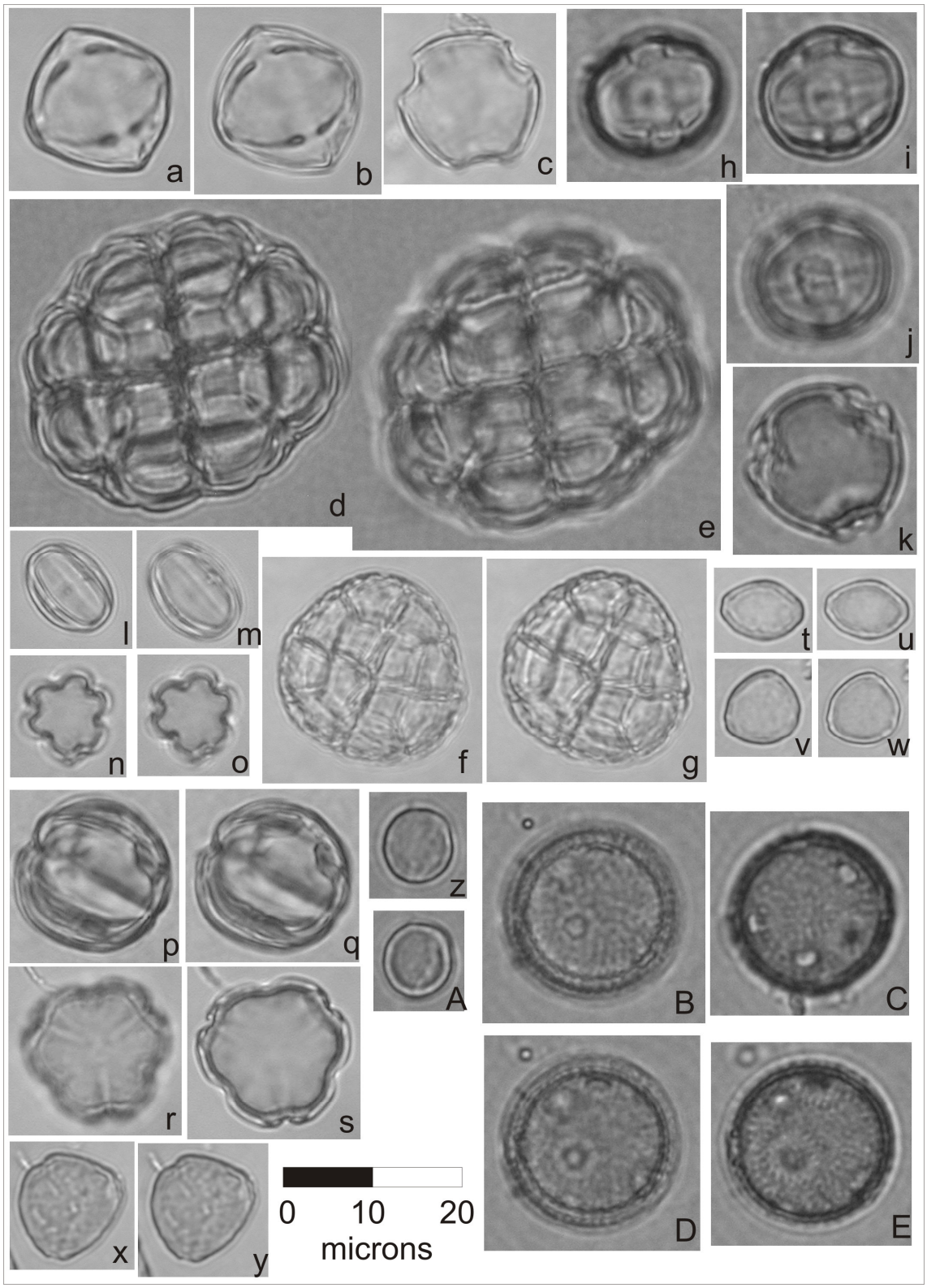
3

1 Figure 4



2

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Figure 5

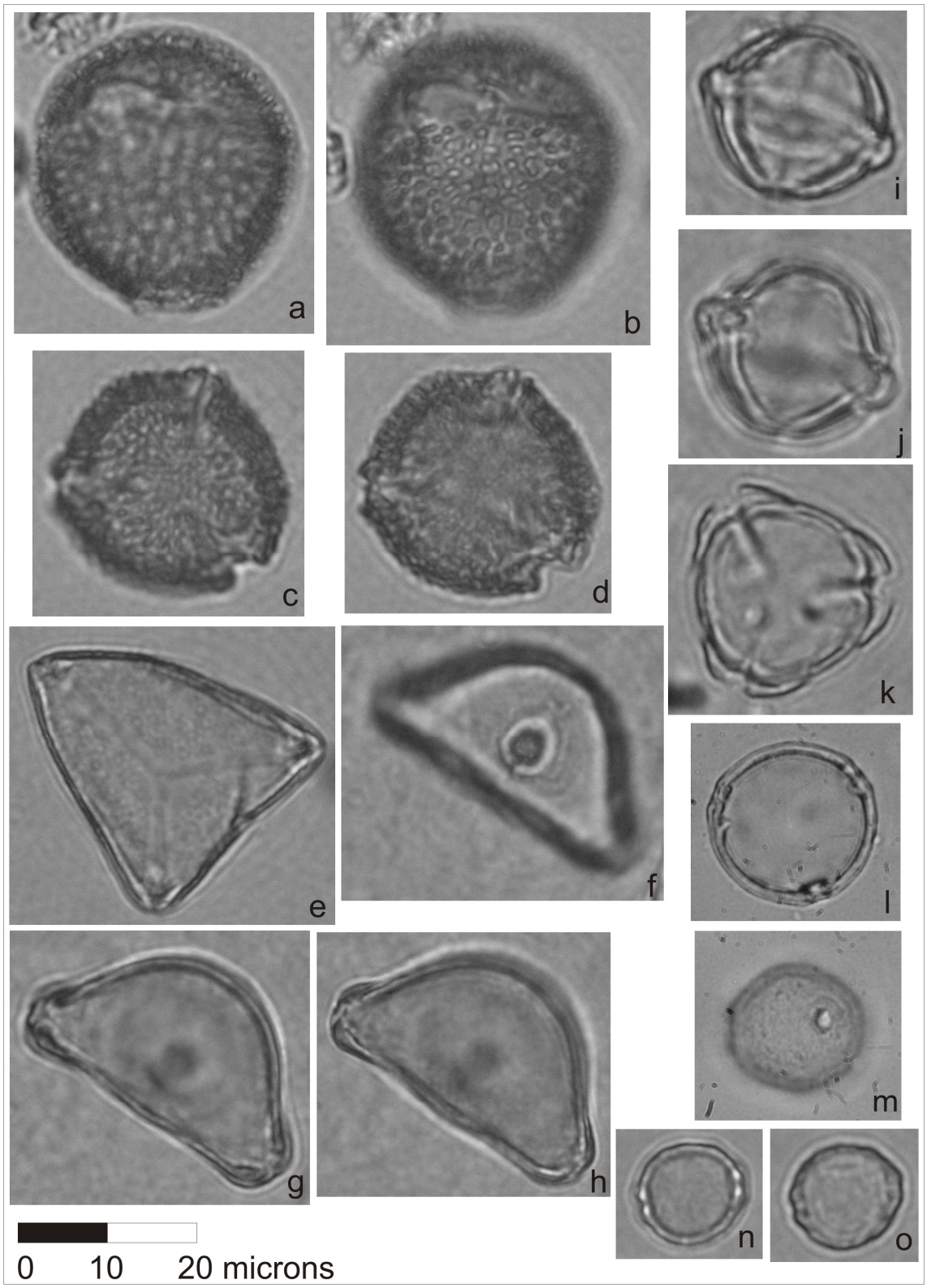

Figure 6